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THE PHYSIOLOGICAL BASIS FOR YIELD DIFFERENCES BETWEEN FOUR GENOTYPES OF GROUNDNUT (*ARACHIS HYPOGAEA*) IN RESPONSE TO DROUGHT. I. DRY MATTER PRODUCTION AND WATER USE†

By R. B. MATTHEWS‡, D. HARRIS, R. C. NAGESWARA RAO§, J. H. WILLIAMS§ *and* K. D. R. WADIA§

ODA Microclimatology Group, School of Agriculture, Sutton Bonington, Loughborough, Leicestershire, England and § International Crops Research Institute for the Semi-Arid Tropics, Patancheru PO, Andhra Pradesh 502324, India

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SUMMARY

Four genotypes of groundnut grown with limited irrigation in a medium depth Alfisol in Central India transpired similar total amounts of water (220–226 mm) over the season, but produced different amounts of shoot dry matter (390–490 g m^{-2}). The extraction front of Kadiri 3 moved most rapidly down the soil profile which may have enabled it to maintain the fastest rates of transpiration when soil water depletion was greatest. Tap root extension rates of Kadiri 3 in the first 32 days after sowing were also the fastest. NC Ac 17090 was more efficient than the other genotypes in extracting water immediately after irrigation from the upper 40 cm of the soil, but this had little value in determining the pattern of water availability in this experiment. Differences in the water extraction characteristics of these genotypes explain little of the variation in dry matter:water ratio, and do not account for the major variation in harvest index associated with drought.

R. B. Matthews, D. Harris, R. C. Nageswara Rao, J. H. Williams y K. D. R. Wadia: *La base fisiológica para diferencias de rendimiento entre cuatro genotipos de cacahuete (*Arachis hypogaea*) como respuesta a la sequía. I. Producción de materia seca y aprovechamiento del agua.*

RESUMEN

Cuatro genotipos de cacahuete cultivados bajo regimen de riego limitado en un Alfisol de profundidad media en la India Central transpiraron cantidades totales similares de agua (220–226 mm) durante la estación, pero produjeron distintas cantidades de materia seca de brotes (390–490 g m^{-2}). El frente de extracción de Kadiri 3 se bajó por el perfil del suelo con mayor rapidez, lo que pudo haberle permitido mantener el ritmo de transpiración más acelerado cuando el agotamiento de agua fue mayor. Los ritmos de extensión de la raíz primaria de Kadiri 3 en los primeros 32 días después de la siembra también fueron los más acelerados. NC Ac 17090 resultó ser más eficaz que los demás genotipos en extraer agua inmediatamente después del regado de los 40 cm superiores del suelo, pero esto tenía poco valor en la determinación del patrón de disponibilidad de agua en este experimento. Las diferencias entre las características de extracción de agua de estos genotipos explican muy poco acerca de la variación de la relación materia seca:agua, y no explican la gran variación en el índice de cosecha relacionado con la sequía.

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‡ Present address: Oxford Forestry Institute, Oxford University, South Parks Road, Oxford, England.

INTRODUCTION

Groundnut (*Arachis hypogaea*) is an important source of oil and protein in the developing countries of the semi-arid tropics (SAT), but average yields may be as low as 0.9 t ha^{-1} in India compared with 2.5 t ha^{-1} in the USA (Gibbons, 1977). Although inadequate fertility and disease protection are important factors (Gibbons, 1980), drought is often the major cause of these low yields.

To stabilize and raise yields in these regions there is a need for genotypes that are resistant to the many different patterns of drought encountered. The world groundnut germplasm collection is held at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), where a number of drought-tolerant genotypes have been identified by field trials using line-source irrigation for screening (ICRISAT, 1984). However, selection for drought resistance has proved difficult because of the large variation in environments between years and sites. This can be overcome by testing large numbers of genotypes in multiple seasons and locations, but this, together with the present procedure of basing selection on measurement of yields at maturity, has proved costly in terms of time and space. Reliable indices of drought resistance are therefore needed to complement conventional improvement programmes.

In this series of papers, we describe types of measurement and analysis which provide a physiological basis for selection based on limited field evidence. Because our own measurements were necessarily confined to a single season, we emphasize that the generalizations made from them should be regarded not as a definitive comparison of genotypes but rather a demonstration of an approach.

The analysis is based on three central relations which have been applied to stands of many arable crops. First, the amount of shoot dry matter (W) removed at final harvest can be expressed as the product of a shoot dry matter:water ratio (q) and the total amount of water lost by transpiration (E). If the harvest index (h) is defined as the ratio of pod yield (Y) to W (i.e. $Y = Wh$) then Y can be expressed as:

$$Y = hqE \tag{1}$$

a form used extensively by Fischer (1978) and others.

A second analogous equation can be written in terms of the solar radiation (S) intercepted by the foliage during the growing season and the amount of shoot dry matter produced per unit of radiation intercepted (e):

$$W = eS \tag{2}$$

Finally, the harvest index specifying the allocation of dry matter to yield at the end of the season can be expressed as a function of a 'partitioning factor' ($p = dy/dw$) which is the instantaneous rate of pod growth (dy/dt) as a fraction

of the corresponding rate of total growth (dw/dt). It follows that, when irrigation is applied over the growing season,

$$h = \frac{\int(dy/dt)dt}{\int(dw/dt)dt} = \frac{\int(dy/dw)(dw/dt)dt}{\int(dw/dt)dt} \quad (3)$$

implying that the harvest index is the mean value over the whole season of the partitioning factor dy/dw weighted by the growth rate dw/dt.

The response of genotypes to their environment may therefore be described in terms of seven parameters - W, q, E, h, S, e and p. The object of the experimental work and subsequent analysis was to determine the relative contributions of these parameters, if any, to the differential drought responses of the genotypes examined.

This paper investigates the relations between the parameters in Equation 1, and considers the possible influence of soil water extraction patterns on each parameter. Subsequent papers examine Equations 2 and 3 in greater detail (Matthews *et al.*, 1988; Harris *et al.*, 1988).

MATERIALS AND METHODS

Genotypes

Four genotypes of groundnut were grown during the post-rainy season (November-March) at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), Patancheru, Central India. Two of the genotypes, TMV 2 and Kadiri 3, are commonly grown by Indian farmers, while the other two, NCAc 17090 and EC76446(292) (hereafter termed NC and EC), were selected on the basis of their contrasting performance in the ICRISAT drought screening programme (ICRISAT, 1984). Kadiri 3 has a duration of about 140 days and the other genotypes 120 days.

Experimental design and crop management

Four replicates of the four genotypes were arranged in a Latin square design. Before sowing, the whole experimental site was irrigated to field capacity and di-ammonium phosphate (18:46:0) applied at 100 kg ha^{-1}. The seeds were sown by hand on 26 November 1982 at 10 cm spacing within rows 35 cm apart to give about 29 plants m^{-2}. After sowing, Alachlor was applied at 1.5 kg ha^{-1}. Mean emergence about 9 days later was close to 80% for all genotypes. The plots were then lightly irrigated every five days until 17 days after sowing (DAS) to ensure uniform establishment. Thereafter, they were irrigated only at 72 DAS and 107 DAS when 65 mm and 85 mm water was applied, respectively. Thus, each genotype was subjected to three cycles of drying and two of recovery between 17 DAS and final harvest at 137 DAS. The final harvest was taken when 70% of the pods were mature.

All plots were regularly hand-weeded and sprayed with either dimethoate or endosulphan to control pests as necessary throughout the season. At 95 DAS,

500 kg ha^{-1} of gypsum (calcium sulphate) was applied to all plots to ensure that calcium deficiency did not limit pod growth.

Growth analysis

From 18 DAS onwards, 10 consecutive plants were removed every week from a previously undisturbed row in each plot. Plants were separated into leaves, stems, pegs, pods and kernels, and the dry weights of these components were measured after drying for 48 h at 105°C. At three-day intervals for the first 32 days after sowing, the entire root systems of three sample plants were removed from the soil by digging an advancing trench along a row of plants. Measurements of tap root length and the number, length and distribution of lateral roots were made.

Water balance

The soil was a medium-depth Alfisol, the upper 30 cm of which was a sandy loam, with a marked increase in clay content with depth. A layer of shingle and decomposed rock was present beneath the clay horizon (Russell, 1978). Volumetric water content of the soil (SWC) was measured weekly at depth increments of 10 cm, using a neutron probe (Didcot Instruments) calibrated against gravimetric measurements in the same field. Four access tubes per plot were installed to depths between 70 and 130 cm. Penetration of tubes below these depths was impossible because of the shingle layer. Water uptake from this layer and below was assumed to be negligible because of its small water holding capacity and high resistance to root growth. The arrangement of access tubes in relation to plant rows was random.

Weekly transpiration (E_p) was determined using the equation:

$$E_p = I + P + \delta S - E_s$$

where I is irrigation, P the precipitation, δS the change in stored soil moisture and E_s the soil evaporation. Irrigation was measured with two buckets placed in each plot. Soil evaporation was estimated by sequential weighing of trays filled with soil, and was found to be negligible two weeks after an irrigation. At each irrigation, there were no significant differences between plots in the amount of water applied or lost by soil evaporation, so plot totals were pooled to give single overall values. Drainage from the profile was accounted for by calculating extraction from a zone when there was an obvious decrease in water content (McGowan, 1974). With the exception of 12 mm of rain at 112 DAS, there was no rainfall during the experiment.

Measurements made by the Soil Physics Section at ICRISAT showed that a soil water potential of −0.003 MPa corresponded to a soil water content of 31.5%. This figure was used as the water content at field capacity, and soil moisture deficit (SMD) calculated as the difference between this and the actual water content.

Environmental measurements

Dry- and wet-bulb temperatures 2 m above the ground were measured with an aspirated psychrometer unit (Delta-T Devices) and incident solar radiation with a Kipp-Zonen solarimeter. Outputs from these sensors were recorded every 30 min throughout the experiment on a data-logger (Campbell Scientific Inc.).

Measurements of evaporation from a Class A pan were obtained from the ICRISAT meteorological station about 0.5 km from the experimental site. Potential evaporation was estimated using the Penman (1948) formula.

RESULTS

Environment

In general, air temperature, saturation vapour pressure deficit (SD) and solar radiation all increased throughout the growing period (Fig. 1), although SD decreased sharply after both irrigations to similar values before rising again.

Total dry matter and pod yields

Kadiri 3 produced the most dry matter and EC the least but TMV 2 gave the highest pod weight despite a low total dry matter (Table 1). This difference was reflected in the harvest indices. Differences between each of these parameters were highly significant.

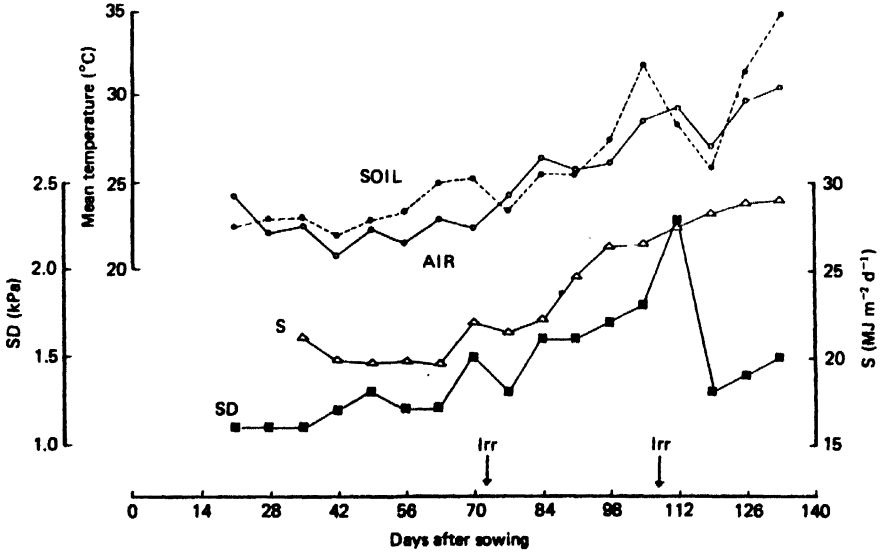

Fig. 1. Summary of environmental variables during the experiment: SD, mean saturation deficit; S, incident solar radiation; AIR, air temperature; SOIL, soil temperature at 5 cm depth; 'Irr' denotes time of irrigation.

Table 1. *Dry weight and water use data of the four groundnut genotypes at final harvest (137 DAS)*

	TMV-2	Kadiri 3	NC	EC	SE
Total dry weight, W (g m^{-2})	424	493	464	389	21
Pod dry weight, Y (g m^{-2})	125	122	93	63	8
Harvest index, h	0.29	0.25	0.20	0.16	0.03
Water used, E (mm)	219	227	228	227	6
Dry matter:water ratio, q (g kg^{-1})	1.94	2.17	2.04	1.71	0.03

Roots

There were no significant differences between genotypes in mean root weight, lateral root length, and lateral root number over the sampling period between 19 and 31 DAS. However, there were differences in the rate of tap root extension (Fig. 2). Values of these rates (cm d^{-1}), estimated from the slopes of regressions fitted for each genotype, were: TMV 2, 0.95 ± 0.15; Kadiri 3, 1.06 ± 0.32; NC, 0.97 ± 0.21; and EC, 0.82 ± 0.14. Only the difference between the fastest, Kadiri 3, and the slowest, EC, was significant.

Water use

In general, rates of transpiration were much slower than rates of potential evaporation, partly because full ground cover was not achieved (Matthews *et al.*, 1988) and partly because of the size of the soil moisture deficit. Potential rates of transpiration were only approached for a few days immediately after irrigation; rates then fell to between 0.15 and 0.3 E_0 as stress became more severe. There were no significant differences between genotypes in the total amount of water used from within the measured soil profile over the growing season.

Differences in water extracted by each genotype from each zone were small and not statistically significant, except for TMV 2 which extracted significantly

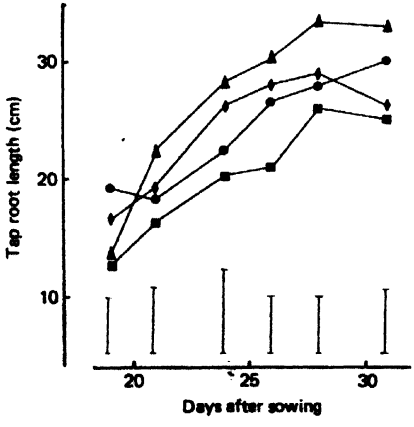

Fig. 2. Changes in tap root length between 19 and 32 DAS for • TMV 2, ▲ Kadiri 3, ♦ NC Ac 17090 and ■ EC 76446 (292). Vertical bars indicate standard errors.

Table 2. *Soil water content (mm) in the top 40 cm for the neutron probe measurement immediately following the irrigations at 72 DAS and 105 DAS for the four groundnut genotypes*

	TMV 2	Kadiri 3	NC	EC	SE
DAS 76	105.9	102.7	99.1	100.6	2.06
DAS 111	100.4	99.0	91.0	96.6	1.97**

** indicates significance at 1% level.

less water from below 40 cm than the other genotypes before the irrigation at 72 DAS.

Differences in the ability of the genotypes to extract water from the surface layers when it was plentiful are reflected in the soil water content of the 0–40 cm zone at the first measurement after each irrigation (Table 2). On both occasions, NC had the lowest soil water content, and TMV 2 the highest, suggesting that the former genotype was better able to extract water from the surface layers. Although these differences were not significant at 76 DAS, they were highly significant at 111 DAS.

The soil water extraction front (WEF) of each genotype was estimated by examining the soil water content as a function of time and noting the time at which there was an obvious reduction in each zone (Fig. 3). Mean values of the rate of descent of the WEF (cm d^{-1}) for each genotype (estimated from the slopes of the regressions) were: TMV 2, 1.13 ± 0.03; Kadiri 3, 1.24 ± 0.03; NC, 1.22 ± 0.04; and EC, 1.12 ± 0.02. The values for Kadiri 3 and NC were not significantly different, nor were those of TMV 2 and EC, but there were significant differences between these two groups ($P < 0.05$). TMV 2 was slowest for

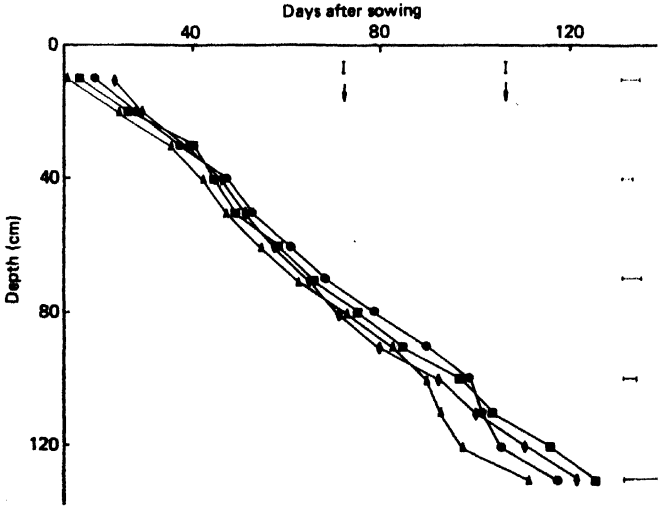

Fig. 3. Changes in depth of the water extraction front with time. Symbols as in Fig. 2.

most of the first part of the season, possibly explaining the smaller quantity of water extracted by this genotype prior to the irrigation at 72 DAS. These WEF velocities are considerably less than those for other tropical crops reported by Angus *et al.* (1983) but similar to the values of tap root extension rate at the start of the season described earlier in this paper.

The rate at which water was subsequently extracted from a zone after the roots reached it could not be estimated with confidence because of the confounding influence of the irrigation at 72 DAS, when water was preferentially taken from the upper part of the profile and extraction rates at depth temporarily slowed. When curves were fitted to the cumulative water extracted from each layer between the irrigations, and a maximum rate of extraction was calculated in the manner described by Landsberg (1977), no significant differences were found between genotypes.

The ability of each genotype to extract water from the total profile in each drying cycle is shown in Fig. 4. The greater SMD for NC at the beginning of each phase, referred to earlier, is reflected in the first values for each drying cycle. There was little difference between genotypes in the water extraction from soil with a low SMD. However, in both drying cycles, EC extracted less water once the SMD became large. Although Kadiri 3 had an initially fast rate of extraction during the first drying cycle, this decreased gradually in a linear fashion as the SMD increased. However, because this decrease was gradual, the rate of transpiration at the end of the drying cycle was faster than for the other genotypes. Kadiri 3 again maintained a greater rate of transpiration towards the end of the second drying cycle.

The limiting SMD at which the transpiration rate is reduced depends on the

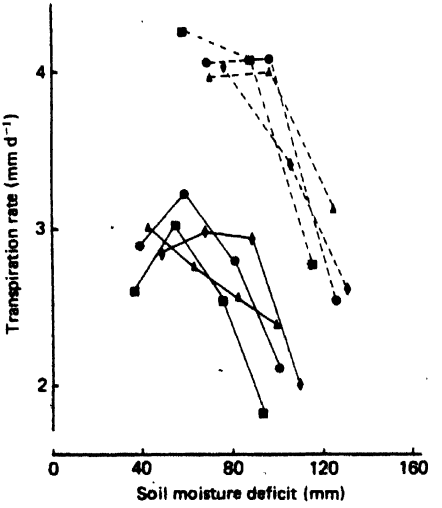

Fig. 4. Relation between soil moisture deficit and transpiration rate; solid lines (———) show period 72–107 DAS, dotted lines (- - - -) the period after 107 DAS. Symbols as in Fig. 2.

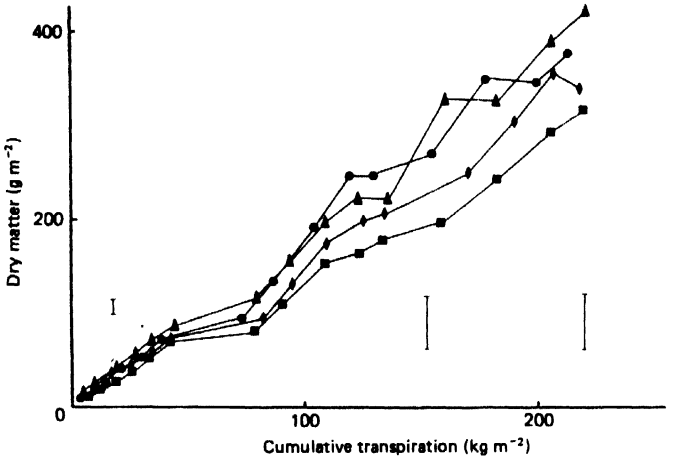

Fig. 5. Relation between accumulated shoot dry matter and cumulative crop transpiration. Symbols as in Fig. 2.

relative sizes of leaf area and the root system. As the season progressed, the limit increased from about 60 mm after the irrigation at 72 DAS to about 100 mm after the irrigation at 107 DAS. By extrapolating the transpiration rates to zero, an estimate can be made of the total water available to the root system. This was about 130 mm in the first drying cycle, and about 170 mm after the last irrigation, when the roots were deeper.

Dry matter:water use ratio

The relation between the total shoot dry matter (including pegs and pods) and the cumulative amount of water transpired (Fig. 5) shows that the only seasonal variations in slope (q) occurred immediately after the irrigations, when there appeared to be a decrease in slope. However, the resolution of weekly growth analysis and transpiration estimates was not sufficient to establish this with confidence. The values of q based on the total dry matter produced and total water used at the end of the season (Table 1) show significant differences between genotypes.

DISCUSSION

Pod weights ranged from 0.6 to 1.25 t ha^{-1} and the crops transpired about 220 mm of water, agreeing well with the data relating yield to water use for groundnut summarized by Boote *et al.* (1982) from several sources. These authors reported that yields increased linearly with water use from zero at about 100 mm to about 4 t ha^{-1} when 500 mm or more was used.

The relative contributions of variation in each of the parameters in Equation 1 to the variation in pod yield can be estimated from the percentage difference

Table 3. *Comparison of parameters for the four groundnut genotypes (EC = 100)*

	TMV-2	Kadiri 3	NC	EC
Pod yield (Y)	198	194	145	100
Transpiration loss (E)	96	100	100	100
Shoot dry matter: water ratio (q)	113	127	119	100
Harvest index (h)	181	156	125	100

of each parameter relative to the values of the lowest yielding genotype (EC) (Table 3). The large differences in Y (98% between best and worst) were due in part to differences in q (27%), but mainly to differences in h (81%).

The variation in q indicates possible scope for the selection of this parameter in breeding programmes, although for this to be practically useful, selection methods suitable for screening large numbers of genotypes need to be developed. The q values obtained were comparable with other values observed in this environment, and slightly less than that observed by Kassam *et al.* (1975), a difference consistent with differences in air humidity (Bierhuizen and Slatyer, 1965). The data were not sufficiently precise to show that seasonal changes in q occurred, although values tended to be smaller immediately after an irrigation when soil moisture was freely available, and greater when the soil had less water.

The differences in q between genotypes were consistent throughout the season and could not be attributed to any temporal differences in water extraction. Neither was there any relationship between q and the size of the soil water reservoir at any time. Kadiri 3 and TMV 2 had the largest values of q, but at any stage had the largest and smallest soil reservoirs, respectively, as indicated by the depth of the water extraction front (Fig. 3). EC with the lowest q did tend to have a less deep WEF. However, Kadiri 3 also had the greatest ability to maintain evaporation from a drier soil (Fig. 4), an attribute which may have contributed to its higher q. EC was least able to extract water when the SMD was large, and had the lowest q; but again TMV 2 with a high q value was not greatly different from EC in its ability to maintain transpiration as the soil dried. Although the range of genotypes is too small to discount the role of roots in resistance to drought, the evidence presented here indicates that rooting characteristics are probably not responsible for much of the variation in q. Other factors, such as the efficiency of the photosynthetic apparatus, may be more influential.

The larger variation in h (Table 3) however, suggests that more progress might be made by selecting for this parameter, a conclusion also reached by Begg and Turner (1976). It has been suggested that h may be influenced by the pattern of water use as determined by the size and distribution of the root system. Early rapid root growth may result in excessive water use during the vegetative period leaving less water for the reproductive period, thus adversely affecting h (Passioura, 1972). For plants growing on stored soil moisture, therefore, both the extent and the timing of root growth may be important.

However, the lack of significant differences between these genotypes in their patterns of water extraction indicates that the major variations in h that occurred in response to drought were not the result of temporal variations in the use of water. TMV 2, which extracted less water from below 40 cm during the first drying cycle, did not use the water conserved at this stage to benefit yield later, although the irrigations may have confounded any potential advantages in this respect. It is more likely that h was influenced by developmental processes (Harris *et al.*, 1988).

NC was able to extract the most water from the surface layer of soil immediately after an irrigation, possibly explaining its relative failure in this experiment compared with other trials where it has performed well (ICRISAT, 1984). NC was selected both in the ICRISAT drought screening programme for superior performance under drought imposed by the line-source technique, where there is a frequent supply of sub-optimal amounts of water to the soil surface, and in field trials at Anantapur, Southern India, where showers are generally light and soils are shallow. The ability to extract this surface water rapidly before it is lost by soil evaporation is clearly an advantage in such conditions, but this ability may have been of little use in the present experiment where deep-rootedness to extract stored water from deep in the profile was advantageous.

These subtle effects of root morphology illustrate the importance of matching genotypes to different conditions of soil and patterns of precipitation. A combination of deep rootedness and the ability to take up surface water rapidly might allow wider adaptation to drought-prone areas, since small showers could be used to maximum effect while the water at depth could be used between major falls of rain. Considerable variation has been found between groundnut genotypes in the depth and length of root systems (Ketring, 1984), which may provide a basis for selection. However, because root measurements are very tedious and expensive, the extent to which root characteristics and water extraction patterns contribute to variations in yield during drought needs to be thoroughly established before major efforts are made to develop large scale screening methods. The evidence presented in this paper suggests that this contribution, at least in groundnut, is small.

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Note. Reference to commercial products in this paper does not imply endorsement or recommendation by ICRISAT in preference to other similar products.

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